Dispatches

Spatial Cognition: A *Tabula Rasa* for the Sense of Direction

Two recent studies have shown that neurons which fire in a compass-like way — head direction cells — are present before rat pups open their eyes. Upon eye opening, the firing direction of these cells is anchored rapidly to visual landmarks.

Paul A. Dudchenko

Let us then suppose the mind to be, as we say, white paper, void of all characters, without any ideas:— How comes it to be furnished? Locke (1690) [1]

A central question in philosophy has recently become a question for neuroscience: what do neural circuits look like before experience with the world? For Locke, the mind before experience was a *tabula rasa* — a blank slate. For Bjerknes *et al.* [2] and Tan *et al.* [3], the mammalian brain possesses a representation of direction even before the animal sees the outside world.

Rats are functionally blind until about two weeks after birth, at which point their eyes open. In their new studies, Bjerknes *et al.* [2] and Tan *et al.* [3] exploited this transition to record from a neural representation of direction in the rat pup brain both immediately before and after the animal opened its eyes. The representation they recorded from, the head direction cell system, is composed of neurons whose firing is tuned to specific directions in the environment. An individual head direction cell typically fires in one direction in the animal's environment, with a range of approximately 90 degrees, and does not fire when the animal faces other directions [4]. However, different head direction cells fire in different 'preferred directions', and these cells appear to form a ring attractor that is anchored to landmarks in the environment [5–7].

Previous work has shown that spatially tuned neuronal activity appears early in the rat's development [8,9]. Specifically, head direction cells show stable directionality at post-natal day 16 of development. Place cells — neurons in the hippocampus that fire when the animal is in a specific location in the environment — are also present from day 16 of development. Grid cells — neurons in the entorhinal cortex and adjacent brain regions that show grid-like tuning fields in the environment — appear at around the same time, but their spatial tuning becomes much sharper by days 24–30 of development. The observation that stable place cell firing precedes stable grid cell fields implies that the former do not necessarily require the latter [9,10].

Do head direction cells require experience to exhibit their compass-like firing? These neurons show a remarkable signal-to-noise ratio, and are found in an interconnected series of brain regions extending from the dorsal tegmental nuclei to the medial entorhinal cortex (MEC) [11,12]. Changes in their firing direction correlate with changes in spatial behaviour [13,14], and damage to the brain regions in which head direction cells are found produce impairments in spatial cognition [15,16].

The results of Bjerknes *et al.* [2] and Tan *et al.* [3] show that direction firing precedes visual experience. Bjerknes *et al.* [2] recorded from the presubiculum, parasubiculum, and medial entorhinal cortex of different rat pups between post-natal days 11 and 15, prior to the opening of their eyes. They found head direction cells in each of these brain areas. The head direction cells, however, showed significant drift in firing directions across the first and second half of a 10 minute recording session, and between adjacent recording sessions. Thus, directionally tuned firing was evident, but was not tied strongly to the environment (Figure 1). Simultaneous recordings of more than one head direction cell showed that the drift in the preferred direction of one cell was similar to that of any other cell. Thus, the cells behaved in the same way, consistent with the idea that head direction cells form an attractor network [17].

Next, Bjerknes *et al.* [2] recorded from the head direction cells just after the rat pups opened their eyes. A basic property of head direction cells is that their 'preferred directions' are anchored to visual landmarks in the environment. The authors found that this was also the case with the rat pups, indicating that the head direction cell system can be anchored to visual landmarks as soon as they are visible.

Tan *et al.* [3] found similar results. They recorded from the dorsal presubiculum and the anterodorsal thalamus in rat pups aged post-natal day 12–20. Before the pups' eyes opened, head direction cells were observed in both brain areas. The cells showed some stability in firing directions within sessions, but this stability was much better once the eyes opened. Interestingly, the percentage of cells showing directional firing increased dramatically once the eyes opened, particularly in the anterodorsal thalamus. Finally, Tan *et al.* [3] also observed that the firing direction of head direction cells was anchored to a visual landmark in a reliable way about a day after the eyes opened. These results suggest that the head direction circuit may rely on some type of non-visual information prior to visual experience, but that visual experience stabilises the representation, and may be critical for the development of a subset of the head direction cells found in the anterodorsal thalamus.

Together, these two studies make several contributions. First, they show that the head direction cell system does not require visual input to form. Head direction cells develop prior to the animal's ability to see the world, and this is consistent with the view that vestibular or other non-visual inputs contribute to the basic directional tuning of these cells [18]. Second, it is clear the link between head direction cells is evident from the start, thus suggesting that the cells function as a coherent network. Third, before visual access to the world the stability of the directional firing, while not entirely absent, is poor. Fourth, when vision

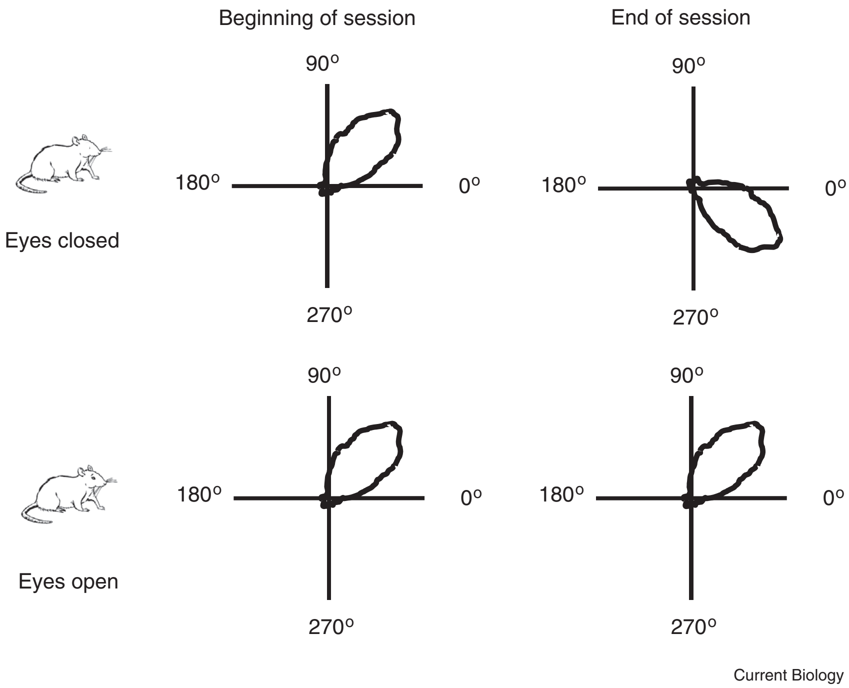

Figure 1. Development of the head direction cell system.

The results of Bjerknes *et al.* [2] and Tan *et al.* [3] show that rat pups have head direction cells before the eyes are opened. Though directional, these cells appear to show within-recording session drift in firing directions. Once the eyes are opened, these cells are much more stable, and are anchored to visual landmarks in the environment.

does come online, the stability of the cells is much improved, and some head direction cells — particularly those in the anterodorsal thalamus — appear to develop directional firing. Finally, the capacity for head direction cells to form an associational anchor to visual landmarks appears within a day of access to these landmarks.

Thus, a blank slate or compass *is* present in the mammalian brain prior to experience with the visual world. With vision, this directional slate is rapidly honed and an associational process allows this internal representation to become linked to the contents of the outside world.

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Olfaction: Smells Like Fly Food

Fruit flies love foods containing yeast. A new study now shows that they are attracted to and have dedicated olfactory neurons for detecting the scents produced by yeast metabolizing common phenolic compounds in fruit.

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A fruit is a tasty, nutritious parcel shaped by natural selection to entice animals to disperse seeds. It is a reward provided by plants containing substances animals need. In fact, fruits have evolved to be nutritious to distract animals from eating seeds and instead move seeds to new habitats away from the parent plant. Fruits are mainly carbohydrates and water, but they also can be a source of fats, proteins, and micronutrients including vitamins, minerals and salts. Their colours and flavours arise mainly from 'non-nutrient' chemicals called phenolic compounds [1]. So far, over 8,000 phenolic compounds have been identified in fruit, vegetables, grains and other plant tissues [1,2]. They function as a form of UV protection